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CAMBRIAN HOLOTHURIANS[1]

AUSTIN H. CLARK

Preface.—In a recent number of *Science*[2] Dr. Hubert Lyman Clark published a most interesting and valuable summary of the literature on the fossil remains of the Holothuroidea, accompanied by critical remarks. The greater part of his paper is devoted to a consideration of Dr. Charles D. Walcott's contribution to the knowledge of Cambrian geology and paleontology in which there are described as holothurians, under the new generic names *Eldonia, Laggania, Louisella* and *Mackenzia,* four new forms from the Middle Cambrian of British Columbia.[3]

Dr. Clark reaches the conclusion that *Laggania* can not positively be assigned to any invertebrate phylum, for he sees "nothing beyond the probable form of the body, and the terminal mouth, to suggest a holothurian, and these characters are equally suggestive of actinians;" *Louisella* he does not believe is a holothurian, though he can offer no suggestion as to its proper systematic position; *Mackenzia* he does not consider a holothurian; he hints that it may be an actinian, though he hastens to emphasize the fact that he does not positively make that assertion; *Eldonia* he is sure is not a holothurian, but he does not place it in any phylum.

To sum up Dr. Clark's criticism, he is sure that none of the four genera established by Dr. Walcott really belong to the Holothuroidea, but he is quite unable to suggest a more logical resting place for any of them.

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[1] Published by permission of the secretary of the Smithsonian Institution who, however, does not hold himself responsible for any of the views expressed.

[2] *Science,* Vol. 35 (N. S.), No. 894 (February 16, 1912), p. 274.

[3] Smithsonian Miscellaneous Collections, Vol. 57, No. 3, pp. 41–58.

Dr. Clark remarks that in Fig. 2 on plate 13 (representing *Mackenzia costalis*) "the terminal mouth surrounded by a jointed or notched ring is distinctly shown; in the specimen I was unable to make out these points satisfactorily"; I can personally vouch for the presence of the "notched ring"; but after the specimen was photographed Dr. Walcott tells me that it was subjected to an acid bath in order to remove a deposit of calcite, and while it was in that bath the ring seems to have disappeared.

Dr. Clark laments that "if *Eldonia* is a holothurian, it becomes virtually impossible to define the class except in terms of the alimentary canal; indeed, if *Eldonia* is a holothurian, the echinoderms themselves can be defined in no other terms, for *Eldonia* lacks every single character which justifies the customary view that holothurians are echinoderms." I can not agree that *Eldonia* lacks every characteristic echinodermal character; but even if it did and we were forced to define the class Holothuroidea on the basis of the digestive tube the Holothuroidea would merely be brought into line with very many of the other animal groups. I would like to see Dr. Clark draw up a definition which would successfully differentiate the Trichoptera from the Lepidoptera, or the Orthoptera from the Neuroptera, or a definition which would include all the members of the Diptera, but exclude all other insects. The more we learn about the various types of animals the more it is impressed upon us that the dividing lines between them are purely arbitrary, and that there is a fundamental unity covering the whole field of zoölogy.

Introduction.—My study of the specimens upon which these new genera and species were based was entirely independent of that made by Dr. Walcott, and, on account of our entirely different previous training, I approached the problems presented in an entirely different way. Excepting *Eldonia,* I did not examine any of the genera in detail until after his paper was in press. After its publication the bearing of these new genera from the Cambrian upon certain phases of marine biology, especially on the probable age of the deep-sea fauna, led me to examine all of them with the greatest care in order to determine to my complete satisfaction whether the classification made by Dr. Walcott was beyond doubt justified by the available facts.

Dr. Clark and I examined the material together during a visit which he made to Washington; but we did not discuss the classification or the systematic position of the genera.

After the publication of Dr. Clark's article, as my examination of the material had led me to conclusions quite different from those at which he had arrived, it seemed advisable to put on record the results of my studies so that those to whom the material is not accessible may have, in addition to the published figures, which are wonderfully good and leave little to be desired, the conclusions of three entirely independent investigators, each with a very different previous training, and each entirely uninfluenced by the conclusions arrived at by the others.

Before taking up the discussion of these forms in detail it is advisable to give a brief outline of the general principles of deduction by which my conclusions regarding them have been reached.

The characters by which animals are identified are of two classes, the fundamental, or characters of prime systematic importance, and the correlative, or characters of prime practical importance, though often of no systematic importance whatever.

In the exceedingly rapid work, often under the most unfavorable conditions, demanded in the identification of organisms brought up by the dredge at sea one has no chance to look for fundamental characters. The general shape of the organisms, coupled with a few other obvious features, alone are depended upon. Thus a shell with a more or less polished surface and perfect bilateral symmetry is at once known to be a brachiopod, regardless of whether it possesses a stalk or not; a soft and flabby, more or less shiny, tubular object, with or without body processes, is at once identified as a holothurian, no matter whether tentacles are visible or not, and quite regardless of its symmetry. In deep-sea work one soon gets to know the representatives of the various phyla by characters never mentioned in systematic treatises, and never even dreamed of by the laboratory student; yet the identification by these characters after practise is quite as sure as the identification by the features of real classificatory significance.

The identification of many fossils calls for essentially the same mental processes as the rapid identification of animals brought up by the dredge; one must be prepared to grasp at once the salient correlative features if the fundamental characters are obscured. Unfortunately this method of work has often yielded deplorable results when applied by paleontologists unacquainted with the practical side of the work of the marine biologist; but this is no reason why it should not lead to perfectly reliable conclusions when logically applied.

The chief of the correlative characters in any group of animals is the general body form taken in connection with the size. Thus in differentiating echinoderms from other organisms at sea we rely entirely upon size and shape; there is no time to look for radial symmetry; we probably take this in subconsciously, though it may be to a large extent mentally ignored.

When any member of a group of animals adopts a mode of life entirely different from that of all the other members of the same group we must be prepared to encounter extraordinary, sudden and unexpected changes in its organization which are not connected with the more usual type of organization by any intermediates; and it must be remembered that such changes affect first of all the general body form. Among such animals we almost always find the group characters developed in a most erratic manner; some structures will be very highly specialized, sometimes specialized far beyond what is seen in any other member of the group, while others will be in a very rudimentary or primitive state of development, or even absent altogether.

The echinoderms differ very abruptly from the crustacean line of descent from which they took their origin and, similarly, each echinoderm class differs very abruptly from all the others. We see in all the echinoderms to-day most perplexing combinations of primitive and highly specialized characters associated in all sorts of ways, and this leads us naturally to the assumption that there was no definite intergrade between the echinoderms and the barnacles, but that the former sprang from the latter or, more strictly speaking, from the same phylogenetic line which may be traced by easy stages to the latter, by a broad saltation in which the assumption of the free habit and the correlated assumption of pentaradiate symmetry combined to make the existence of intergrading forms impossible, while at the same time it resulted in the formation by the echinoderms, at the very moment of their origin, of two widely diverse stocks, the heteroradiate (including the Pelmatozoa, the Echinoidea and the Holothuroidea) and the astroradiate (including the Asteroidea and the Ophiuroidea) between which there are, and can be, no intergrading forms.

Thus in dealing with the echinoderms we must be ever on the alert to detect sudden saltations. We must also be prepared to eliminate from our minds all ideas of hypothetical ancestors from which all echinoderms are commonly supposed to have been derived, but which probably never existed; and, along with the hypothetical ancestor myth, to banish from our thoughts all ideas of fundamental echinodermal structures, equally non-existent. No echinodermal structure is of such fundamental importance in the economy of the animals that it can not be either profoundly modified or even dispensed with altogether under special conditions, reverting to a type more or less characteristic of some other phylum. The pentaradiate symmetry is often brought forward as a character of the highest importance; but it is the result not of a class peculiarity, but of simple mechanics; the somatic divisions in the echinoderms are marked by lines of weakness; hence the divisions of the body must be uneven in number, so that no line of weakness will go straight through the body, thus subjecting the animal to danger through a shearing strain; when the somatic divisions are by lines of extra strength, as in the cœlenterates, the divisions are always equal, as in this case the continuation of a line of strength directly across the body gives added rigidity.

We know enough about organic life at the present day to be somewhat sceptical when new phyla are proposed to include problematical forms. If we can not allocate an animal on the basis of some supposedly fundamental character, or if it falls on the basis of a single character in a phylum from all the groups in which it differs in all the others, we ignore that character entirely and take up another. In every group each character has a definite and restricted application, beyond the limits of which it is quite valueless. The echinoderms are commonly said to be pentaradiate, and the great majority certainly are; but certain genera, entirely or in part, possess three, four (like most medusæ), six, seven, eight or ten rays; we recognize them as echinoderms just the same. Specimens of the genus *Limnocnida* are commonly pentaradiate; but we instantly recognize them not as echinoderms, but as hydromedusæ. The echinoderms we say have abundant calcareous deposits in the skin, and often also in the deeper parts of the body; the genus *Pelagothuria* has no trace of any calcareous deposits whatever, but no one doubts that it is an echinoderm.

These few obvious cases are selected from an almost unlimited choice; they show conclusively that any character, no matter how fundamental it may be, may suddenly become quite worthless, forcing us to depend entirely upon other characters which in other cases are more or less ignored. Thus, to take two instances from the fossil crinoids, in the genus *Marsupites* the only feature which can possibly give a clew to its true affinities is the arm structure, which is that of an ordinary comatulid; and in the allied genus *Uintacrinus* the arm and pinnule structure alone are found to be reliable.

Eldonia.—In *Eldonia* there are only two structures upon which we can hope to base our deductions concerning its systematic position: (1) the bell-like general shape, and (2) the coiled digestive tube with two tentacle clusters at the anterior end.

1. The bell-like shape suggests the cœlenterates, and such forms as *Trochosphæra* or trochophore larvæ.

The highly specialized digestive tube at once negatives the supposition that *Eldonia* may be a cœlenterate.

Trochosphæra has a general form and an internal structure which is certainly suggestive of *Eldonia;* but there are many reasons why it is not possible to connect the two. In the first place there is the question of animal mechanics; the size of the members of each group of animals is limited by physical and mechanical considerations due to the requirements of fundamental structure, etc. Thus we do not find butterflies as large as ordinary birds, nor cetaceans so small as the average fish; their structure is not adaptable to the limitations imposed by such sizes. *Trochosphæra* is surrounded by a band of cilia, just below which is the mouth, and below that another band of cilia. Ciliated bands do not transform into broad body fringes such as we see in *Eldonia;* they are more or less uncertain structures, and are present as ciliated bands, or are absent altogether. *Trochosphæra* has a powerful retractor muscle attached to the posterior portion of the alimentary canal; powerful retractor muscles are a feature of all the rotifers; there is no trace of any retractor muscle in *Eldonia.*

In *Trochosphæra,* and in the so-called trochophore larvæ, the anus opens at the pole determined by the ciliated band as the equator, while the mouth is just below the chief ciliated band. In *Eldonia* the mouth is the more central, and there appears to be a possibility that the anus is on the dorsal surface above the fringed border. The ciliated bands of *Trochosphæra* have a very definite connection with the mouth, a connection not evident between the fringed border of *Eldonia* and the mouth, the relationships in the latter being almost exactly like the relationships between the digestive tube and the expanded brim in such holothurians as *Euphronides tanneri.* Although the superficial resemblance between *Eldonia* and *Trochosphæra* (including trochophore larvæ) is certainly striking, I can not see the slightest reason for connecting the two; the relation between them is precisely similar to that between certain of the pteropods and the nautilus, which, on account of their remarkable similarity, were for a long while placed in the same genus.

2. Certain "worms" have a digestive system suggesting that of *Eldonia;* but such worms are never provided with oral tentacles, possessing instead a tough protrusible proboscis; nor do they ever have the digestive tube differentiated as in *Eldonia;* nor do they ever have the body of a type which, on account of the structure of the body wall and the general internal anatomy, particularly the type of muscular investment, could by any stretch of the imagination be supposed to assume a bell-like form.

Certain heteroradiate echinoderms, as some holothurians belonging to the family Elpidiidæ, a few echinoids, and the (recent) endocyclic crinoids, have a digestive tube resembling very closely that of *Eldonia,* and in the holothurians there are always tentacles about its anterior end. Moreover, in many of the Elpidiidæ, as, for instance, in *Euphronides tanneri,* the body is entirely surrounded by a broad brim with marginal lappets, just as it is in *Eldonia.*

Judging from all the evidence which we have—and the specimens of *Eldonia* are among the most wonderfully preserved fossils which have ever come to light—*Eldonia* can be nothing else than a heteroradiate echinoderm, and among the heteroradiate echinoderms a holothurian, in which class it comes nearest to certain of the Elpidiidæ.

Affinities of Eldonia.—In *Eldonia* the body is medusa-like, circular, bordered with a broad *Euphronides*-like brim of uniform width; the mouth and anus are near together, the mouth being nearer the center; the general configuration of the digestive system is very similar to that seen in the endocyclic crinoids; there are two large many-branched tentacles, one on either side of the mouth.

Eldonia seems to me to be a pelagic derivative from some elpidiid type; the body has shortened so that the mouth and anus have become closely approximated; the brim surrounding the body has become laterally extended and uniformly developed, so that a swimming bell has resulted. *Eldonia* is therefore an elpidiid holothurian which has become flattened dorsoventrally and at the same time laterally expanded into a circular form resembling that of the medusæ.

We are familiar with just such a transformation in the echinoids; *Dendraster, Echinarachnius, Arachnoides,* etc., are flattened, circular and disk-like, though derived from ovoid, globular or more or less spherical types. In these the flattening has been in the direction of the radial symmetry so that the oral pole is at or near the center of one surface and the aboral pole at or near the center of the other. In *Eldonia* the flattening has possibly, though not certainly, been in a plane at right angles to this so that the oral pole is at one edge of the circular disk and the aboral pole at the other. This is only a slight advance over the conditions seen in *Benthodytes typicus,* so that it need occasion no surprise.

The reduction of the number of tentacles in *Eldonia* to two possibly indicates a suppression of three of the radial systems, leaving only two of the original five. Many of the crinoids show a more or less complete reduction of two or three of the radial systems; indeed, in *Tetracrinus* one is invariably absent.

In certain forms among the Comasteridæ, as, for instance, in *Comătula micraster,* ambulacral grooves, nerves and tentacles may be entirely absent from six out of the ten arms, or from three out of the five rays, leaving, as in *Eldonia,* only two of the original five divisions functioning normally, and these two may be three times as large as the others.

If we can assume that the two tentacles of *Eldonia* indicate a suppression of three of the original five radial systems, or a carrying out to completion of the condition already far advanced in many of the Elpidiidæ, a reasonable explanation of the structure of *Eldonia* becomes a relatively simple matter.

If we take a form like *Scytoplanes typicus* or *Euphronides tanneri* and shorten the body so as to bring the mouth and anus near together, giving the digestive tube exactly the same shape that it assumes in the so-called endocyclic crinoids, the two radial muscles would form a circular band of concentric muscle fibers just beyond the enteric canal, exactly as we see them in *Eldonia.*

Ordinarily among the echinoderms the mouth is at one pole of the radial symmetry and the anus is at the other. In the recent crinoids the anus has become entirely dissociated from the aboral radial pole and has migrated to a position near the mouth. It is thus evident that the connection between the anus and the aboral pole is not absolutely unchangeable.

The water vascular system centers, in all echinoderms, in a ring about the œsophagus, from which (usually) five radial canals are given off. How then can we account for the small central ring in the center of *Eldonia,* far removed from the mouth? The first question to be answered is whether the arrangement of the water vascular system about the mouth is really fundamental, or whether it is merely a matter of mechanical convenience when the mouth happens to be, as it usually is, at or near one of the apices of the pentamerous symmetry.

Now among the crinoids there are two families, the

Comasteridæ and the Uintacrinidæ, in which the mouth, instead of being as usual in the center of the ventral surface of the disk, is lateral, situated typically on the very edge of the ventral surface of the disk, between the bases of two of the arm groups. In these families the tubes of the water vascular system, above which ambulacral grooves usually, though not always, run, instead of converging in five large vessels to the circumoral ring lead from the arms to a large trunk vessel which runs around the periphery of the disk with the anal tube instead of the mouth as its center. This large peripheral ring, is interrupted posteriorly, and the mouth passes through it anteriorly; but it indicates a tendency for the water vascular system to transform from a ring about the mouth to a ring about the anal tube, or more correctly, into a ring about the ventral pole of the body regardless of the position of the mouth. In this connection it would be interesting to determine if in the Comasteridæ the so-called stone canals were confined to the circumoral ring, or if they showed a tendency to migrate secondarily along the peripheral water tube.

With the assumption by *Eldonia* of the circular form and the spiral digestive tube the muscles assumed a concentric arrangement. Probably at the same time the water tubes, following the course of the muscles, also attained the form of a peripheral canal, after the same manner as we see almost consummated in the Comasteridæ. The peripheral water tubes in *Eldonia* serve largely as braces to bind the animal together, just as they serve as braces in the marginal brim of *Euphronides tanneri*. This function would, for mechanical reasons, induce a diminution in the diameter of the central ring, in order that they might function to the best advantage; but the muscular ring, in order to preserve a maximum availability for expansion and contraction, would remain with the greatest possible diameter. Thus we should theoretically reach a condition precisely like that seen in *Eldonia;* a very large concentric muscular ring, and a very small, also concentric, apical water vascular ring with exceedingly long tubes reaching out into the marginal tube feet, fused together into a broad and uniform marginal brim.

In *Eldonia* the radial canals so-called are the canals of the podia transformed into a system of braces, exactly as they are transformed into a system of braces in *Euphronides tanneri, Benthodytes typica,* and many similar forms; in these species, which live supported upon ooze and have developed a broad brim about their body so that they will not sink into it, the ring canal of the water vascular system retains its original position about the œsophagus, while in *Eldonia,* which floats free in the water, and possesses a medusoid body form, the canals have become enormously elongated and of uniform length all around, serving as body supports (like the ribs of an umbrella) instead of merely as supports for an expanded brim; and, as a necessary result of the change in the mechanics of the body, the central ring of the water vascular system has migrated from its original position about the gullet to an apical position in the center of the apical portion of the animal, equidistant from the border on every side.

The entire dissociation of the water vascular system from the mouth is the most difficult thing to explain in *Eldonia.* But, after all, this is not without a parallel. In the bilaterally symmetrical invertebrates one of the most fundamental structures is the nerve ring about the œsophagus, consisting of the supraœsophageal ganglion, the two circumœsophageal ganglionic connectives and the subœsophageal ganglion. The relationship of these nerves is entirely changed in the crinoids; here we find a circumœsophageal ring consisting of the supraœsophageal ganglion alone, the subœsophageal ganglion at the dorsal pole, with its continuation directly downward at right angles to the plane of the digestive canal instead of parallel to and directly beneath it, and the circumœsophageal ganglionic connectives resolved into numerous nerve strands parallel to, instead of passing horizontally around, the gullet. Surely if such a fundamental rearrangement can take place in the nervous system we can not be surprised in seeing the water vascular system become entirely dissociated from the mouth.

Pelagic animals tend to become delicate and translucent, and if belonging to groups with a more or less calcified (or chitinous) skeleton, to reduce that skeleton to a minimum or to dispense with it entirely. Thus the entire absence of any trace of a skeleton in *Eldonia* does not prevent us from suggesting an affinity with the holothurians, more especially as the recent pelagic holothurian *Pelagothuria* has no trace whatever of calcareous elements.

Dr. Clark remarks that the oral tentacles of *Eldonia* are suggestive of the marginal clusters of *Lucernaria* and its allies, or perhaps are not fundamentally different from those of some rhizostomous medusæ. This would naturally be the case no matter to what group *Eldonia* belonged. The tentacles of *Eldonia* undoubtedly are subject to the same mechanical and physical forces as are those of the pelagic medusæ, and this would be amply sufficient to induce a strongly marked parallelism, no matter what their ultimate origin might have been.

The body of *Pelagothuria* is tubular, with the mouth at one end and the anal opening at the other; its alimentary canal is in loops (a long-drawn-out spiral); the swimming organ is merely an expansion of the oral disk. *Pelagothuria,* therefore, though similarly pelagic, is radically different from *Eldonia,* derived from a radically different stock.

The embryology and metamorphosis of the echinoderms lead us to believe that they were derived from phyllopod crustacean ancestry through the barnacles as a result of the sudden suppression of one half of the body and the consequent assumption of a circular body form. Since there are only two tentacles in *Eldonia,* we might suggest the remote possibility that *Eldonia* may have arisen from a form like *Scytoplanes typicus* by a further sudden suppression of half of the body and the dropping out of three of the rays, the rest of the body curving about so as to form again a circular animal from one originally pentamerous, though ultimately derived from bilateral ancestors.

Louisella.—No marine animal is known except among the Elpidiidæ with a body form resembling that of *Louisella pedunculata.* A comparison between this fossil and such recent species as *Scotoplanes insignis* shows a similarity that can not but be more than superficial.

Dr. Clark in speaking of *Louisella* says that "none of the podia are sufficiently defined to enable one to make out even the form, let alone the structure, whereas if they were really like those of *Scotoplanes* and other elasipods, their rigidity would have caused them to be as well defined as any part of the body outline." Every one who has collected specimens of certain of the species of Elpidiidæ knows that they are as delicate and as difficult to preserve as are many, if not most, medusæ; even when hardened in alcohol the podia of such forms as *Deima pacificum* are extremely soft and flabby. If any species of the group adopted a pelagic habit this character would naturally be greatly accentuated.

Laggania.—It is difficult to see how *Laggania cambria* can be interpreted otherwise than as a holothurian of the elpidiid type, a form related to such species as *Benthodytes sanguinolenta,* or especially to *B. sibogæ.*

Circumstantial Evidence Suggesting the Possible Occurrence of the Elpidiidæ in the Palæozoic.—As I understand the three holothurians from the Middle Cambrian described by Dr. Walcott (*Eldonia, Laggania* and *Louisella*), they all fall within, or are closely related to, the family Elpidiidæ. Now the Elpidiidæ are preeminently creatures of the deep sea, and represent possibly the most strictly abyssal group to be found among marine organisms. The *Siboga* dredged one species in 31 fathoms, and the first species to be described was found in

50 fathoms in the Arctic Ocean; but the great majority of the species occur below 1,000 fathoms, extending downward to 2,900 fathoms.

Now in forms confined to the deep sea, or to exceedingly high latitudes, or subjected to widely varying temperatures or salinities, or occurring in highly saline, alkaline or acid water, or under unnatural conditions generally, the geological age of the maximum virility of the genera or families may be guessed by the amount of difference between the chemical and physical surroundings among which they now live, and the conditions obtaining slightly below low-tide mark on a tropical coast bathed by ocean water free from any admixture of fresh, and containing the normal proportion, in amount and in kind, of salts. Such forms as *Artemia,* occurring in salt pans, *Xiphosurus, Tachypleus* and *Carcinoscorpius* (*"Limulus"*) occurring in more or less foul and muddy situations, and the Elpidiidæ, characteristic of great depths, we therefore suspect of being relics of the earliest geologic times, representing what were once the dominant types in their respective groups, possessed of such vigor and adaptability that, forced by internal specific pressure, due to increase in the number of the individuals, they were able to accommodate themselves to these conditions. When these types began to wane new and vigorous forms arose in the tropical littoral which extirpated them from all the more desirable locations, allowing them to persist only in such unnatural situations as those into which they had intruded when in the prime of their vigor.

There is not the slightest reason for supposing that any markedly new animal type ever originated in the deep sea, or under conditions differing much from those found just below the low-water mark.

If we are ever to discover any recent representatives of such groups as the trilobites, the eurypterids, the blastoids or the cystids we shall find them not in the tropical or temperate littoral, but living under some highly abnormal conditions, in the deep sea, in highly saline, alkaline or acid water, in the regions of excessive cold or excessive heat (such as hot lakes), in stagnant pools in the ocean bed, in brackish underground lakes or streams, or in comparable situations; but apparently none of these groups were highly adaptable; though very abundant, they flourished through comparatively small extremes in their physical and chemical environment, from which subsequent vigorous types with the same or a greater economic radius promptly ousted them.

The disappearance of a group in a given horizon, it should be pointed out, does not at all mean that the group really vanished at that time; it means merely that at that time it disappeared from the littoral. Most groups undoubtedly persisted long after they ceased to occupy a habitat which is now a geological stratum, under locally unfavorable conditions, finally dying out at a time long subsequent to the last record in the rocks.

Not only does the deep-water habitat of the Elpidiidæ betoken a very ancient origin, but the group to-day is evidently senescent. The extraordinary shapes assumed by most of the species can only be interpreted as a result of an explosion of the characters induced by extreme age.

Thus, reasoning backward from a study of the recent fauna alone, we should expect to find the Elpidiidæ and *Artemia*, or very closely allied forms, in the early paleozoic rocks, representing the littoral in the age when they were at the height of their ascendancy, and we should be greatly surprised should they appear in any post-paleozoic formation.

Lorenzinia.—*Lorenzinia*, mentioned by Dr. Clark, is undoubtedly the cast of part of a medusa, as any one acquainted with the literature on the fossil medusæ can see.

Mackenzia.—The two specimens assigned to the genus *Mackenzia* appear to me to be undoubtedly mud-living actinians of the family Edwardsiidæ, closely related to the *Edwardsia,* for the following reasons. In a semi-desiccated synaptid the longitudinal lines marking the longitudinal muscles become gradually obsolete, and the digestive tube, more or less distended with inorganic matter, becomes more and more prominent, so that finally we see an elongated worm-like object with a prominent digestive tube which bears a collar about the anterior end; longitudinal markings become obliterated and lost in the irregular foldings which take place, while these also obscure the other more flaccid internal organs; a soft mud-living actinian, on the other hand, is reinforced internally by numerous mesenteries; on desiccation these tend to lie flat, and to raise the body wall at the lines of attachment slightly, giving a fluted or pleated appearance, just as is shown in *Mackenzia.* No trace of a tubular digestive tube is visible in *Mackenzia,* nor is there any other internal differentiation, but there are prominent, regular and numerous parallel pleats; these pleats are four in number in the upper part of the body, but apparently five in the lower part, so that there are probably eight mesenteries represented; there appear to have been sixteen tentacles, two in each intermesenterial space; the contracted lower portion of the body suggests the physa of *Edwardsia;* it is probable, therefore, that *Mackenzia* is an actinian, and that it should be placed in the family Edwardsiidæ near the genus *Edwardsia.* Some of the preserved specimens of *Edwardsia farinacea* in the National Museum collection are almost identical with the specimen of *Mackenzia costalis* figured by Dr. Walcott, the similarity of the contracted anterior portion of the body being especially striking.

Systematic Position of the Genera Discussed.—When a biologist, especially a zoogeographer, undertakes to deal with fossils, he becomes of necessity somewhat of an iconoclast. The faunas of the several horizons represent to him not so many distinct and separate successive faunas each derived directly from that preceding, but so many distinct faunal regions, each equidistant from the center, the center representing the phylogenetic starting point of organic life. In certain limited genera or in certain small groups an extraordinary progressive development is undoubtedly traceable through a greater or lesser extent of geologic time; but in general there is a balance between the organisms in each horizon which is strikingly similar to the balance between the organisms in every other horizon and between the organisms in each of the present faunal regions, so that, taking into consideration the circumstances under which the animals in each horizon lived, we are not able to say with any degree of accuracy that, phylogenetically speaking, any one fauna, zoogeographic or paleontologic, is *in toto* more primitive than any other.

Keeping this in mind and speaking solely as a biologist, I would suggest the following disposition of the genera described by Dr. Walcott:

- Holothuroidea
  - Family Elpidiidæ
    - Genus *Laggania*
    - Genus *Louisella*[4]
  - Family Eldoniidæ (near the Elpidiidæ)
    - Genus *Eldonia*
- Zoantharia
  - Family Edwardsiidæ
    - Genus *Mackenzia*

Summary.—*Eldonia* is a free-swimming holothurian, and is most closely related to the species of the family Elpidiidæ.

In body form alone does *Eldonia* resemble a medusa; this general resemblance may therefore safely be disregarded as a parallelism resulting from a similar pelagic habit.

In the general shape of the body as well as in the course of the digestive tube *Eldonia* approaches *Trochosphæra* (and trochophore larvæ); but the enormous discrepancy in size, the broad fringe about the body, the large tentacles on either side of the mouth, the absence of muscles of the group type characteristic of the rotifers, and the submarginal anus, seem to negative the idea that the two can be in any way related.

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[4] Both of these genera can probably be referred, with a reasonable degree of probability, to subfamilies in this family; but it seems best to leave them, for the present at least, unassigned.

The medusoid body form, the absence of a protrusible proboscis and the presence of a large branched tentacle on either side of the mouth appear to offer conclusive evidence that *Eldonia* can not be a "worm."

The digestive tube of *Eldonia* resembles that of the heteroradiate echinoderms, and especially that of certain holothurians; the tentacles on either side of the mouth suggest an affinity with the holothurians; the radial canals, leading to a central ring, are comparable to the radial canals and the central ring of the holothurians; the broad circular muscle about the body suggests a modified longitudinal holothurian muscle, and is of the group type characteristic of the echinoderms; the broad brim about the body is strikingly similar to the brim developed in certain elpidiid holothurians, such as *Euphronides tanneri* and *Scytoplanes typicus*. A pelagic holothurian is known as an inhabitant of the recent seas; though very different in origin and in affinities from *Eldonia*, it demonstrates that a pelagic habit is not impossible in the group. The species of the family Elpidiidæ are preeminently inhabitants of the deep sea; this suggests that the fossil representatives of the family should be found in very early geological formations.

Therefore *Eldonia* is a pelagic holothurian, related to the species of the family Elpidiidæ.

No marine animals are known outside of the holothurian family Elpidiidæ which have a body form like that of *Louisella pedunculata* in all its details; but this species agrees in every particular with one or other of the species in that family. We can not, therefore, escape the conclusion that *Louisella pedunculata* should find a place in the family Elpidiidæ along with all the recent animals which in any way resemble it.

By exactly the same reasoning *Laggania cambria* is assigned to a position in the same group.

The type specimen of *Mackenzia costalis* shows a pleated structure which can only be interpreted as due to longitudinal mesenteries, probably eight in number; there appear to have been sixteen processes around the mouth which probably indicate tentacles retracted before preservation; the distal portion of the body resembles closely the distal portion of the body in the genus *Edwardsia*. Thus, as *Mackenzia costalis* presents characters not found outside of the Zoantharia, and in that group peculiar to the family Edwardsiidæ, it seems necessary to assign it to a position in the family Edwardsiidæ, near the genus *Edwardsia*.